Potential of an Unnatural Host, *Galleria mellonella* (Lepidoptera: Galleriidae), in Rearing the Corn Earworm Endoparasitoid *Microplitis croceipes* (Hymenoptera: Braconidae)

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ABSTRACT Females of the endoparasitoid *Microplitis croceipes* (Cresson) oviposited in early 5th instars of an unnatural host, greater wax moth, *Galleria mellonella* (L.), after they had been treated with hemolymph and frass from the natural host corn earworm, *Helicoverpa zea* (Boddie). Third-instar *H. zea*, similar in size to 5th-instar *G. mellonella* were used for comparison. Forty-one percent of the *G. mellonella* larvae were accepted for oviposition, and 90% of 3rd instars of the natural host. Parasitoid cocoons weighed 8.30 ± 0.34 mg (mean ± SE) compared with 14.08 ± 0.16 mg from *H. zea*. Adult emergence was 46.9 and 92.6% on *G. mellonella* and *H. zea*, respectively. The sex ratio of parasitoids reared on *G. mellonella* (40% male to 60% female) was not significantly different from parasitoids reared on *H. zea* (35% male to 65% female). F_1 adults reared on *G. mellonella* were smaller than those reared on *H. zea*. When the F_1 progeny of *G. mellonella*-reared parents were reared back on the natural host, *H. zea*, the resultant adult parasitoids were of normal size.

KEY WORDS *Galleria, Microplitis, Helicoverpa zea*, in vivo, rearing, parasitoid, atypical host

Microplitis croceipes (CRESSON) is an important solitary endoparasitoid that attacks the corn earworm, *Helicoverpa zea* (Boddie), and the tobacco budworm, *Heliothis virescens* (F). Mass rearing of *M. croceipes* is of great interest in agriculture because of its potential use in biological control of *Heliothis* species (Knipling and Stadelbacher 1983). However, rearing *M. croceipes* on the natural host for pilot field releases is too costly (Powell and Hartley 1987, Greany et al. 1989, King and Coleman 1989). Although several species of insect parasites have been successfully cultured on semidefined and defined media (Grenier et al. 1994), none of the hymenopteran larval endoparasites such as *M. croceipes* have been reared from egg to adult in vitro (Greany 1986, Thompson 1986, Rotundo et al. 1988, Ferkovich and Oberlander 1991, Pennacchio et al. 1992, Ferkovich et al. 1994). Presumably, this is because the endoparasitoid union with host physiology, and because of its need for specialized growth factors (Greany 1986, Ferkovich and Oberlander 1991). Vinson and Iwantsch (1980a) reported that the ability of an endoparasitoid to survive in a host depends on the suitability of the host in terms of evasion of the internal defensive systems of the host, competition with other parasitoids, toxins detrimental to the parasitoid egg or larva, and adequate nutritional support of the parasitoid. In addition, parasitoid ability to survive in a host also depends on its ability to regulate host development for its own benefit by inducing physiological and biochemical changes in the host (Vinson and Iwantsch 1980b). This raises the question of whether an endoparasitoid such as *M. croceipes*, which has specific physiological requirements, could be successfully reared from egg to adult on an atypical host.

Atypical hosts have been used in studies on rearing beneficial ectoparasitoids (Debach 1964, Maltby et al. 1973). In particular, greater wax moth, *Galleria mellonella* (L.), was a suitable substitute host for the ectoparasitoid *Archytas marmoratus* (Townsend). High yields of the parasitoids (57%) resulted on full-grown larvae, whereas attempts to rear the parasitoid in vitro on artificial diet were unsuccessful (Coulibaly et al. 1992, Bratti 1993). We recently examined 6 species of Lepidoptera for possible use as atypical hosts for rearing *M. croceipes* (Ferkovich and Blumberg 1994). From the standpoint of host acceptability, all the atypical hosts were acceptable for oviposition after treatment with frass and hemolymph from *H. zea*. However, successful development of the parasitoid occurred only in *Galleria mellonella* and to a lesser extent in the fall armyworm, *Spodoptera frugiperda* (J. E. Smith). In the current study we focused on the development of *M. croceipes* from egg to adult in *G. mellonella* and compared it with development in the natural host, *H. zea*.

Table 1. Comparison of *M. croceipes* parasitoids reared on typical and atypical hosts

	Typical host *H. zea*	Atypical host *G. mellonella*
	Dissected hosts	
% parasitization	90.0 ± 1.7 (83/92)a	41.3 ± 5.0 (62/150)b
No. eggs/host	1.73 ± 0.14a	1.0 ± 0.0a
Wt/cocoon	14.08 ± 0.16 mga	8.30 ± 0.34 mgb
	Hosts held for parasitoid development	
% adult emergence[a]	92.6 (100/108)	46.9 (15/32)
% female emergence	65.0 (65/100)	60.0 (9/15)
% male emergence	35.0 (35/100)	40.0 (6/15)
Life cycle	12–15 d	21–28 d

Within a row, means followed by similar letters are not significantly different at $P = 0.05$ level.

[a] Percentage of adult emergence was calculated from the total number of cocoons obtained, 108 and 32 from *H. zea* and *G. mellonella*, respectively.

Materials and Methods

Host and Parasitoid Colony Maintenance. *H. zea* was reared according to Lewis and Burton (1970) at the Insect Biology and Population Research Laboratory, USDA–ARS, Tifton, GA. We received eggs by mail and allowed them to hatch on *Heliothis* Premix diet (Stonefly Industries, Bryan, TX). *G. mellonella* was reared according to Bean and Silhacek (1989). *M. croceipes* was reared as described earlier (Ferkovich and Dillard 1986) with the following modifications: two 3-d-old female parasitoids were added to each cup of 40–50 late 2nd- and early 3rd-instar *H. zea* for 24 h. Larvae were then removed and individually placed in 28 g plastic cups with 4–5 ml of semisolid diet and kept at 25°C and 60–70% RH for 14 d. Parasitoid cocoons were then removed and placed in emergence cages for 3 wk. Adults were removed daily and kept at a sex ratio of 1:1. At 2 d after emergence, males were discarded and the females kept for colony maintenance and research. Finally, chloramphenicol was not added to water vials as described earlier.

Experimental. Fifth-instar *G. mellonella* (27.3 ± 0.9 mg [mean ± SD] per larva) were treated with ≈1 μl hemolymph taken from a clipped proleg of early 4th-instar *H. zea*. Fifth-instar *G. mellonella* were used because they were similar in size to 3rd-instar *H. zea* (28.0 ± 1.4 SD mg per larva). The treated larvae were then placed into culture dishes (100 by 15 mm) that had a light coat of *H. zea* frass from 5th instars smeared on the bottom of each dish. The larvae were then exposed to 3- to 4-d-old female *M. croceipes* for 1 h under a fluorescent lamp. The female parasitoids used had been previously exposed to males but not to hosts. At the end of exposure the parasitized larvae were returned to diet and incubated at 30°C and 70% RH. Third instars of the typical host, *H. zea,* were exposed to the female parasitoids at the same host to parasitoid ratio as that used for *G. mellonella.* Two sets of 10–15 replications (10 larvae in each replication) were stung for both *G. mellonella* and *H. zea.* One set was dissected 15 d after sting and held to determine percentage of parasitism, and the other set was held to determine percentage of emergence. A 2nd experiment was designed to find out if the progeny of *G. mellonella*-reared adults would result in parasitoids of normal size on the natural host, and to compare fecundity and the rate of parasitization of *H. zea*-reared females with *G. mellonella*-reared females. Sixty *H. zea* larvae were exposed to *H. zea*-reared females and 30–51 *H. zea* larvae were exposed to *G. mellonella*-reared females at a ratio of 10:5 hosts: parasitoids at parasitoid ages of 1–6 d. Fewer hosts were exposed to the *G. mellonella*-reared females at a given time because fewer females were available. Measurements were made of the forewings and metathoracic femora and tibiae of males and females of *H. zea*-reared and *G. mellonella*-reared parasitoids.

Statistical Analysis. Data were analyzed by 1-way analysis of variance (ANOVA) and means were separated by the Tukey–Kramer test using Instat software (GraphPad 1993). All significance reported is at the $P = 0.05$ level.

Voucher specimens of all 3 species are designated for deposit in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL.

Results

Sex ratios were similar, parasitism and average cocoon weight less, and developmental time longer in *M. croceipes* reared from the factitious host, *G. mellonella* than from the natural host, *H. zea* (Table 1); and *G. mellonella*-reared parasitoids were smaller than *H. zea*-reared parasitoids (Fig. 1 A–C). Although the adult females were smaller, they readily attacked *H. zea* larvae and produced healthy 1st instars (Fig. 1D). *G. mellonella*-reared females also parasitized the natural host, *H. zea,* as well as *H. zea*-reared females, except at 1 and 6 d after eclosion (Table 2). The number of larvae dissected from *H. zea* parasitized by *G. mellonella*-reared and *H. zea*-reared parasitoids was 205 and 113, respectively. Based on measurements of forewings, and femur, tibia, and cocoon weights, F_1 *G. mellonella*-reared parasitoids were significantly

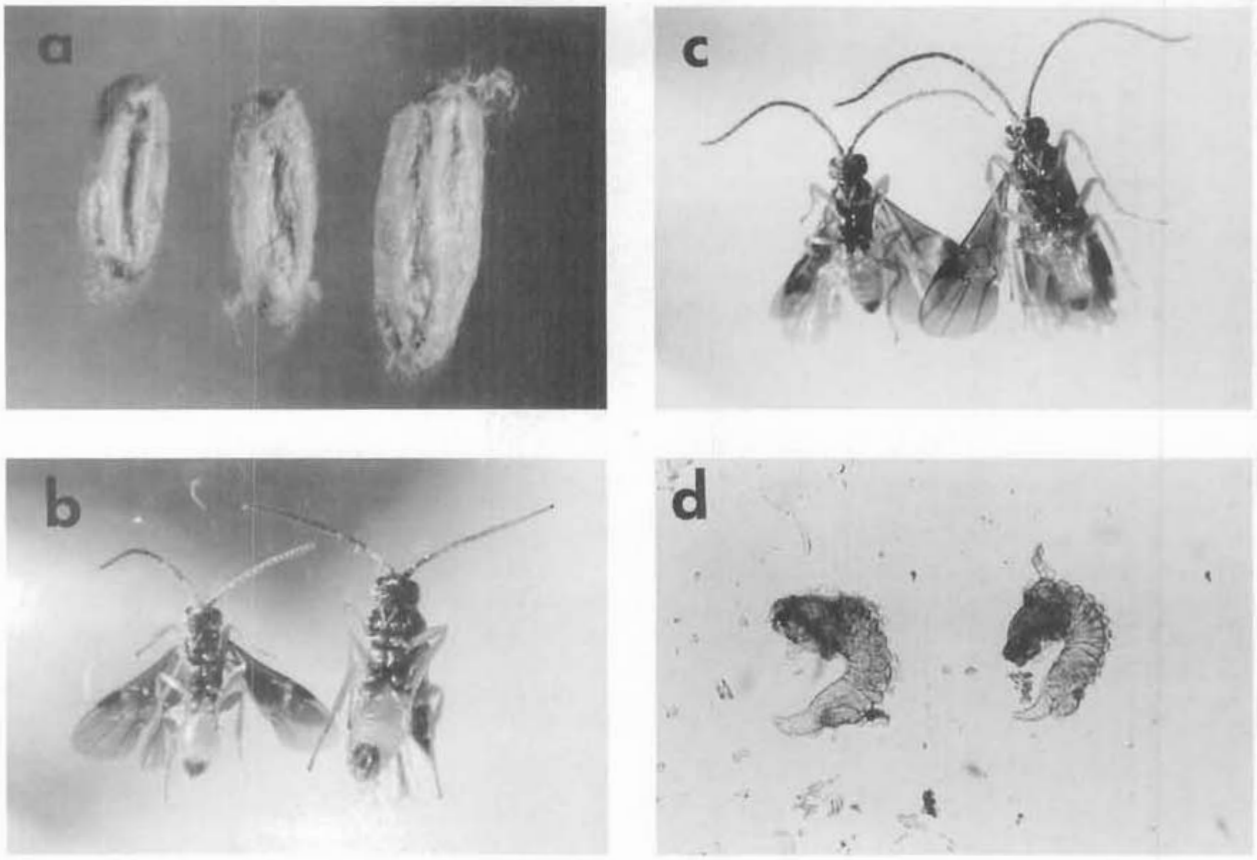

Fig. 1. (a) Size differences of *M. croceipes* cocoons (2 on left, *G. mellonella*-reared), (b) adult female, and (c) adult male reared on *H. zea* (right) and on *G. mellonella* (left). Magnification 18.4×. (d) First instar parasitoid of *G. mellonella*-reared female dissected from *H. zea* larva (right) and 1st-instar parasitoid of *H. zea*-reared female also dissected from *H. zea* (left). Magnification 40×.

smaller than *H. zea*-reared parasitoids (Table 3). This size distinction was eliminated, however, when *Galleria*-reared parasitoids were reared to the F_1 generation on the natural host, *H. zea*.

Discussion

In the field, *M. croceipes* is a solitary endoparasitoid that spends part of its life developing in the hemocoel of natural hosts, *Helicoverpa* and *Heliothis* species. That *M. croceipes* can be reared on an unnatural host, *G. mellonella*, is interesting from the standpoint of the requirements for the success of the parasitoid–host relationship. Doutt (1959) divided the events into the following 4 steps: (1) habitat location, (2) host location, (3) host acceptance, (4) host suitability; and Vinson and Iwantch (1980b) added an additional step, (5) host regulation. In the current laboratory study, we first had to induce parasitoid females to oviposit into *G. mellonella* larvae, which were otherwise unattractive to female parasitoids. This was accomplished by treating *G. mellonella* larvae with host hemolymph, as previously reported (Ferkovich and Blumberg 1994). However, the rate of parasitism in *G. mellonella* was ≈50% less than in the natural host.

Although we were not able to develop a continuous strain of *M. croceipes* on *G. mellonella*, we did obtain a sufficient number of F_1 generation parasitoids on *G. mellonella* to rear back on *H.* zea. The resultant lower rate of parasitization on day 1 in *G. mellonella*-reared F_1 females probably reflects the lack of experience on the original host, because the same females were used for each age and this difference disappeared as the females became experienced. That the parasitoids reared on

Table 2. Comparison of the rate of parasitism of *H. zea* larvae by *H. zea*-reared *M. croceipes* females and *G. mellonella*-reared females

Age, d	% parasitism	
	H. zea-reared	*G. mellonella*-reared
1	41.7 ± 5.4 (26/60)a	25.0 ± 5.0 (13/51)b
2	46.7 ± 2.1 (28/60)a	38.7 ± 5.1 (15/38)a
3	70.0 ± 2.6 (42/60)a	75.0 ± 3.9 (33/44)a
4	61.7 ± 1.7 (37/60)a	66.7 ± 7.5 (22/33)a
5	65.6 ± 4.3 (39/60)a	51.5 ± 5.9 (16/31)a
6	82.5 ± 2.5 (33/40)a	46.6 ± 3.3 (14/30)b

The same females were used to sting host larvae on the days indicated. Fewer hosts were stung at each age with *G. mellonella*-reared females because low numbers were available. Within a row, means followed by similar letters are not significantly different at $P = 0.05$ level.

Table 3. Size distinction of *M. croceipes*-reared on *H. zea*, *G. mellonella*, and *G. mellonella*-reared parasitoids reared back on the typical host, *H. zea*

Parent host F_1 host	*H. zea* *H. zea*	*H. zea* *G. mellonella*	*G. mellonella* *H. zea*
Wings			
Male	4.55 ± 0.01a	3.69 ± 0.01b	4.61 ± 0.01c
Female	4.34 ± 0.01a	3.51 ± 0.05b	4.36 ± 0.01a
Femur			
Male	1.07 ± 0.009a	0.84 ± 0.01b	1.11 ± 0.004a
Female	1.09 ± 0.01a	0.87 ± 0.01b	1.14 ± 0.005a
Tibia			
Male	1.49 ± 0.01a	1.18 ± 0.01b	1.53 ± 0.006a
Female	1.50 ± 0.004a	1.18 ± 0.01b	1.61 ± 0.007c
Cocoon wt, mg	14.08 ± 0.15a	8.33 ± 0.34b	14.90 ± 0.10a

Wing, femur and tibia lengths given in millimeters and cocoon weights in milligrams. Within a row, means followed by similar letters are not significantly different at $P = 0.05$ level.

G. mellonella still preferred the natural host supports the view of King and Morrison (1984), that entomophagous arthropods reared on an unnatural host for a short time will probably respond as usual to the natural host.

The lower numbers of *M. croceipes* produced on *G. mellonella* reflect the inferior suitability of it as a host rather than a low rate of host acceptance. In a related study, treating *G. mellonella* larvae with freeze-dried hemolymph of *H. zea*, which contains concentrated ovipositional stimulating kairomone (Heath et al. 1990), resulted in a rate of oviposition similar to that in the natural host, but it did not increase the percentage of adult emergence beyond that obtained in this study.

The frequency of parasitoid egg encapsulation by a host insect is considered an important factor in determining the suitability of a host (Blumberg 1990). Blumberg and Ferkovich (1994) reported that *G. mellonella* was most suitable for the development of parasitoid eggs and less suitable for the development of parasitoid larvae, hemocytic encapsulation in *G. mellonella* occurred only in the larval stage of the parasitoid. This is in contrast to the beet armyworm, *Spodoptera exigua* (Hübner), another atypical host, in which 100% of the eggs dissected from parasitized hosts were encapsulated. Polydnaviruses play an important role in abrogating the immune response to the parasitoid in certain parasitic hymenopterans (Fleming 1992). Edson et al. (1980) demonstrated that co-injection of purified polydnavirus with washed virus-free *C. sonorensis* eggs in the compatible host, *H. virescens*, not only prevented encapsulation but also allowed normal development of wasps to the adult stage.

That *M. croceipes* can be successfully reared on *G. mellonella*, an unnatural host, indicates that virus was partially effective in suppression encapsulation in *G. mellonella*. This raises the question of whether the polydnavirus is expressed to the same level and in the same tissues in *G. mellonella* as in *H. zea*. Injection of the polydnavirus associated with the ovaries of *M. croceipes* reduced growth and development in *G. mellonella* as compared with that in *H. zea* (unpublished data). Yet Hayakawa et al. (1994) reported that DNA purified from polydnavirus of the parasitoid wasp, *Cotesia kariyai* (Watanabe), was expressed in hemocytes of the permissive host armyworm, *Pseudaletia separata* (Walker), and prevented growth and development of the host. In contrast, the virus was expressed only at a low level in larval hemocytes of an unnatural host, the common cutworm, *Spodoptera litura*, and did not prevent normal development in this insect.

Even if the parasitoid is able to overcome host encapsulation response, humoral factors (for example, cecropins, atacins), could have inhibited development of the parasitoid embryo (Dunn 1986) or the nutritional environment for the parasitoid may not have been suitable for its normal growth and survival (Vinson 1984). The rate of development of *M. croceipes* was slower on *G. mellonella* than on the natural host, *H. zea*. In general, this finding is typical of the slower rate of growth of parasitoids on factitious hosts (Maltby et al. 1973, Minot and Leonard 1976, Wallner and Grinberg 1984). That the smaller F_1 parasitoids reared on *G. mellonella* were still able to parasitize the natural host successfully and produce progeny of normal size, suggests that the hemolymph of *G. mellonella* probably lacks adequate levels of essential nutrients or specific growth factors (Ferkovich and Oberlander 1991). Bloem and Duffey (1990) stated that the growth and development of an endoparasitoid *Hyposeter* exiqua (Viereck), was regulated by the nutritional status of its hosts, *H. zea* and *Spodoptera exiqua*. Likewise, Ritter and Johnson (1991) reported that sterol levels in the hemolymph of *H. zea*, effected by the addition of cholestyramine to its diet, increased larval developmental time and resulted in adults that were significantly smaller than the controls. The requirement for specific growth factors or nutrients by *M. croceipes* in this study is also suggested by in vitro

developmental studies. The parasitoid never molted or developed beyond the 1st instar in vitro although the larvae were robust and lived far beyond the normal developmental time of 5–6 d for 1st instar in vivo (Ferkovich and Oberlander 1991). Coar and Greany (personal communication), however, found that 1st-instar *M. croceipes* molted into 2nd instars in vitro only if they were dissected from *H. zea* host larvae when they had attained a size >3mm in length.

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